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Theme session H: Evolutionary effects of exploitation on living marine resources

**Effects of fisheries on energy- and sex-allocation
in slow-growing hermaphrodites such as groupers**

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Introduction

Harvest often affects abundance and population dynamics of the targeted species, but effects may be different and more diverse for hermaphrodites compared to dioecious species. One effect of harvest is that it normally truncates age- and size-distributions (Jennings et al. 2004), which in the case of sequential hermaphrodites can virtually remove one of the sexes (Alonzo and Mangel 2004). The severity of this effect depends on how flexible the sex changing rule is (Alonzo and Mangel 2005). In shrimp, the proportion of early maturing females (individuals that skip the male phase and reproduce as females already in their first reproductive season) responds to the composition of the population, and is higher in years when many females have been removed by fishing (Charnov 1982).

Fishing is identified as a potential cause for driving evolution towards earlier maturation in many fish stocks and has been suggested to lead to earlier sex change in sex-changing species such as groupers. Many studies have focused on the ecological effects of fisheries on sex-changing fish (Alonzo and Mangel 2004, 2005), but little attention has been directed towards understanding the evolutionary responses to high and size-dependent fishing mortality .

Our motivation for this study is a rapidly expanding export-oriented grouper fishery in the Maldives that began in mid 1990s (Shakeel and Ahmed 1996). The abrupt intense fishing activity on many species of groupers resulted in the fishery reaching its peak in 1997, and with no management in place catch rates have since declined. Also for the nassau grouper *Epinephelus striatus* in the Caribbean, the numbers of both spawning fish and spawning aggregations have decreased since fisheries began (Sadovy 2002). Groupers are slow-growing, long-lived and late-maturing species (see Heemstra and Randall (1993) for a review of the biology of groupers). They inhabit coral-rich areas of lagoon and seaward reefs in almost all tropical and temperate areas at depths ranging from 4 to 100 m and feed mostly on crustaceans and small fishes (Heemstra and Randall 1993). This model is parameterized for *Epinephelus fuscoguttatus* (common names: brown

marbled grouper or flowery cod). This species matures around ~ 9 years of age and may reach ages of ~ 40 years and lengths up to 100 cm (Pears et al. 2006). Similar to sharks and rays, the slow life histories make groupers highly susceptible to over-fishing (Stevens et al. 2000), and this effect is amplified by the high market demand and export prices reaching \$100 per kg.

The model

We have developed an evolutionary individual-based model of emergent size at maturity and energy allocation under varying levels of fishing mortality. In the model, three genes differ between individuals: size at maturation, and energy allocated to reproduction in male and female phase, respectively. A genetic algorithm then finds evolutionarily stable life history strategies in an evolving population under various levels of fishing mortality and selectivity. Males have a slight size advantage and generation are overlapping.

Results

Our results predict that the life history traits are quite sensitive to even low fishing mortalities (Fig. 1). Age and length at both maturation and sex change decrease in the population with increasing fishing mortalities (Fig. 2). The model predicts shifts (at the population level) between a hermaphroditic and dioecious strategy with increasing fishing mortalities (see caption to Fig. 1), as well as decreasing population size and increasing female to male sex ratios with fishing effort. Yield peaks at low to intermediate levels of fishing mortality (about 0.08 year^{-1}).

Discussion

The population is quite sensitive to fishing mortality, and life history evolution takes place at even low fishing mortalities. Increased fishing mortality leads to a strategy where individuals mature and change sex at earlier ages and smaller sizes.

The model predicts that for situations with no or low fishing mortalities, females follow a hermaphroditic strategy, where they allocate energy to both growth and reproduction simultaneously. This trade-off between growth and reproduction ensures that the individual continues to grow in the initial sex (i.e. female for protogynous hermaphrodites). As female fecundity increases with size, reproduction at larger sizes increases their reproductive success in the female phase, as well as their potential reproductive success in the male phase.

As fishing mortality increases, the energy allocated to reproduction in the female phase shows that the population shifts from a hermaphroditic via a dioecious and back to a hermaphroditic strategy (Fig. 1). Dioecy can be explained by the concept of 'early maturers' (Charnov 1982) (i.e. 'early maturing males' for groupers) where some individuals mature or breed for the first time as males and do not undergo any reproduction in the female phase. In reality these are pure males, allocating no energy to reproduction in the female phase and using their energy budget to increase size and reach the male phase. In the same populations, females tend to allocate more of their energy to reproduction, meaning that they grow less and have a lower probability of reaching the sizes where they would change sex to become males.

That fisheries may select for earlier maturation and smaller sizes has previously been found by empirical and theoretical studies. This study suggests that fisheries may also change the breeding system itself, which may have large implications for population dynamics, stability and extinction risk. Whether this may happen also in nature depends on how flexible the evolution of mating systems is.

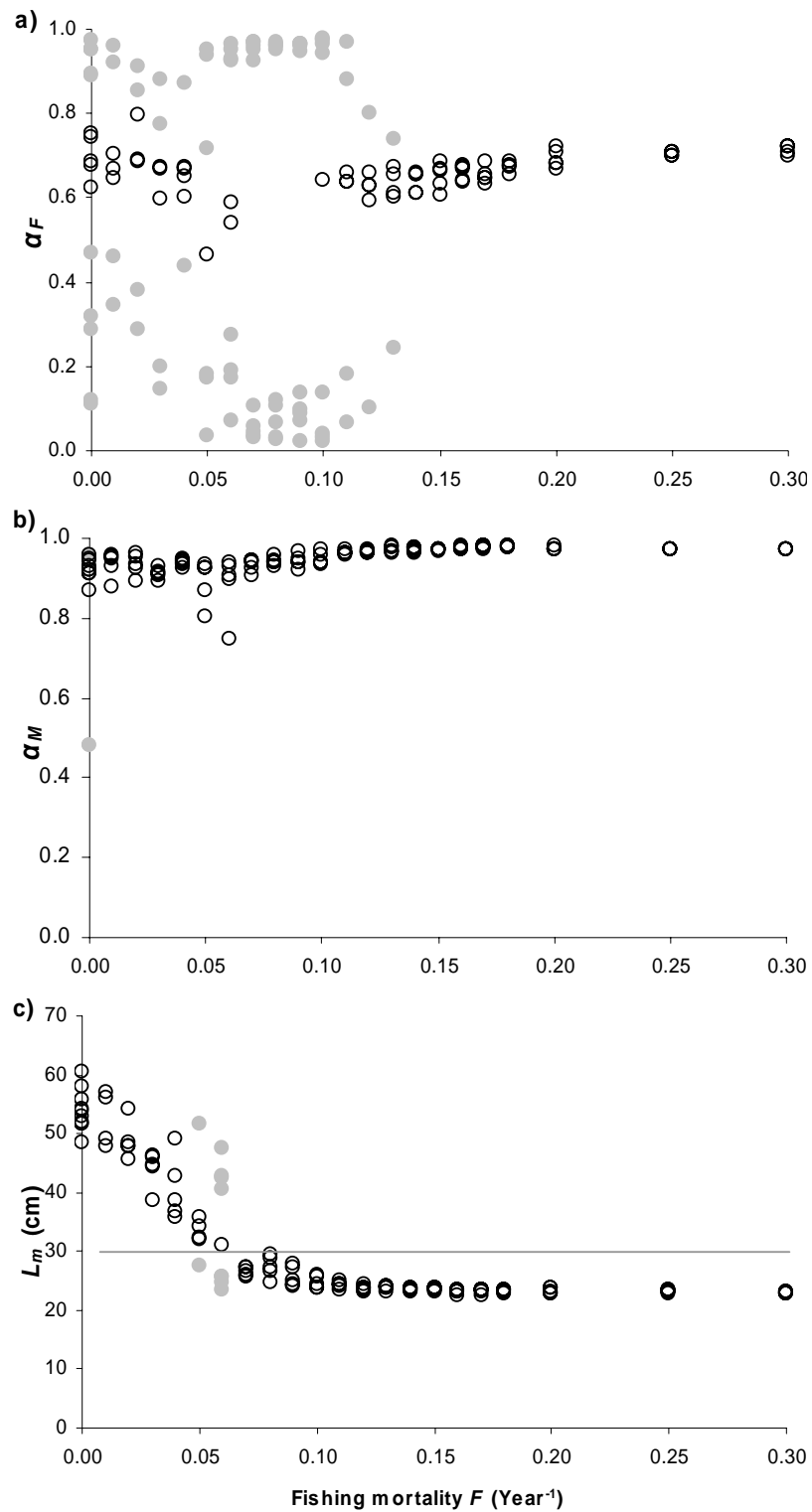


Figure 1. Evolved genotypes coding for life history strategies in a grouper population (*E. fuscoguttatus*) subjected to harvest. Each open circle indicates on replicate simulation, and grey circles represent peaks in a bimodal distribution of trait frequencies. Fishing selectivity was set at 50% at 30 cm (indicated by grey line) and increasing rapidly above that. Energy allocation to reproduction in the female phase α_F (a), energy allocation to reproduction in the male phase α_M (b) and length at 50% probability of maturation L_m (c). Notice that the allocation to reproduction in the female phase changes between hermaphroditic strategies (values between 0 and 1) at low fishing mortalities, via dioecious life history strategies (either ~ 0 or ~ 1) at intermediate fishing mortalities, and back to a hermaphroditic strategy when the life history has evolved to maturation and sex change below the sizes fished at high fishing mortalities.

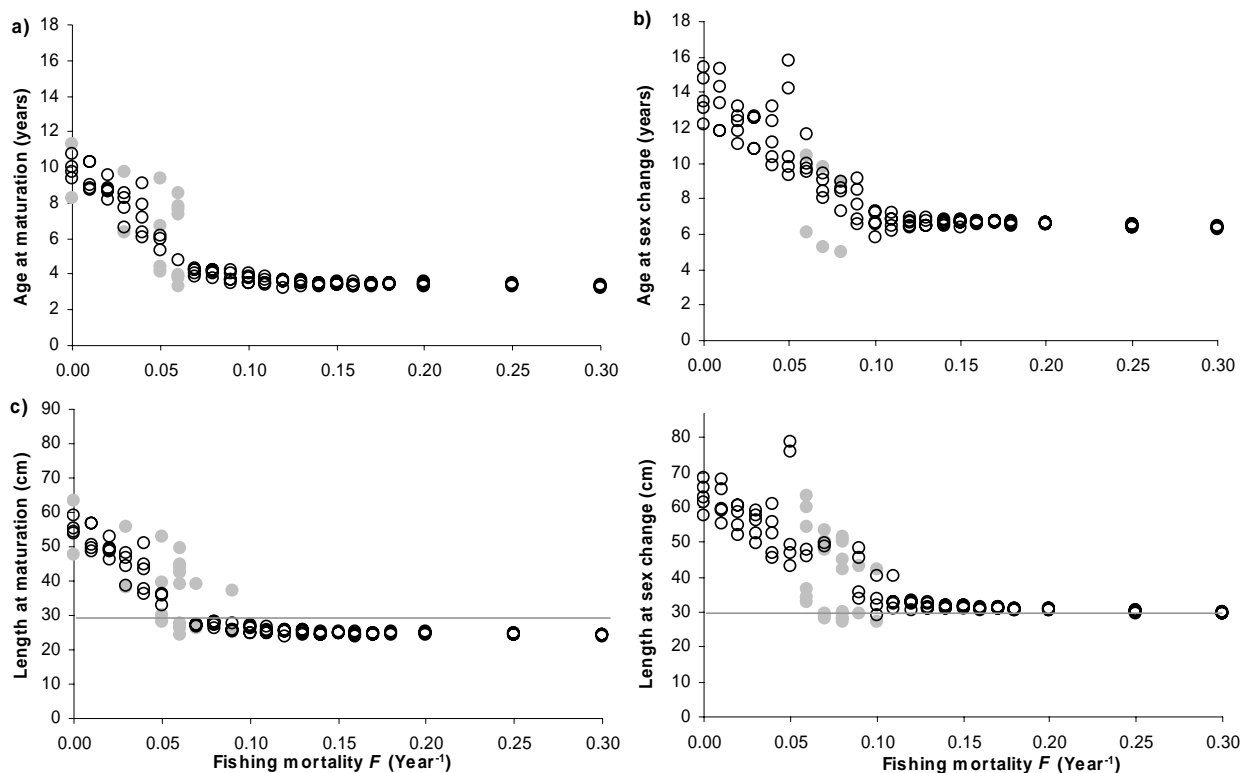


Figure 2. Evolved phenotypes (life history strategies) for a grouper population (*E. fuscoguttatus*) subjected to varying levels of harvest intensity. Mean values for age and length at maturation and sex change at different fishing mortalities and fisheries selectivity as in Figure 1 (the size of 50% catchability by the fisheries is indicated by the grey horizontal line). Age at maturation (a), age at sex change (b), length at maturation (c) and length at sex change (d).

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